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ENVIRONMENT AND DISEASE

A Discussion on the Parasitism of *Armillaria mellea* Vahl. Fr.

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PREDISPOSING FACTORS AND TYPES OF ENVIRONMENT.

THE environment of a forest tree presents an extremely complex problem for examination, and it is only rarely that in the study of disease the environmental factors acting as its primary causes are so obvious as to be capable of immediate discovery. An attempt will be made to define what a primary cause of disease is, and to give the distinction between this and a factor predisposing to disease. A primary cause of disease is any factor in the environment, which in the development of a diseased state, is the first to bring about a morbid condition. A factor predisposing to disease, however, in no way tends in itself to bring about such a condition: it merely makes it possible for a primary cause to do so. Thus in Britain early flushing in exotic conifers is a factor predisposing to damage by late frost, the primary cause of disease. Again, cloudy weather may be a factor predisposing pines to infection by *Cronartium ribicola* (20) in that it provides the conditions necessary for the successful production and distribution of the infecting basidiospores. Such examples might be multiplied indefinitely, and it is obvious that, if disease is to be controlled, both the predisposing factors and its primary causes must be understood. A second distinction is also necessary. It must be possible to distinguish between the factors acting as primary causes and those acting subsequently and in a secondary manner. Thus the crown of a tree severely affected by drought may be rapidly killed back by a bark-infesting fungus, which would be unable to attack a tree in full vigour. The factors concerned with disease may thus, by the adding of one factor to another, become numerous, and it is not always the most obvious that are the most important.

In considering environment in relation to disease it will also be of service to state what types of environment occur. First, there are two main types, the biological and the physical, and disease may arise owing to adverse factors in either of these or in both acting together. The physical environment is again of two kinds, edaphic and climatic; and again disease may be due to adverse edaphic or climatic factors acting separately or together with or without the interference of biological factors. Apart from all this there are the inherent characteristics of the forest tree to be taken into account. Disease is always produced by the interaction between the host and one or more of the types of environmental factor enumerated above, and it is to be prevented by removing or avoiding the adverse factors, or by producing a race of tree capable of withstanding them without injury.

THE PARASITE AND ENVIRONMENT.

The plant parasites causing forest diseases may be divided into classes according to the extent to which they depend on the pre-existence of a morbid condition in the host in order to be able to live upon it. Certain fungi appear able to parasitize a perfectly healthy tree; the rusts and mildews provide examples of this. A certain state in the host or condition in the environment may be necessary to successful infection, but such state or condition does not involve the host being diseased: it is merely susceptible and nothing more. It is probably true, however, that the majority of cryptogamic parasites are more easily able to attack and to develop within a host that is in a morbid condition than in one that is perfectly healthy, and it is certain that some parasites have very little power to do damage unless such a condition exists. Now, although we are not much accustomed so to think of it in Forestry, such a morbid condition, however slight it may be, is essentially a state of disease. The factors that bring it about are the primary causes of disease, and their relation to the host needs to be understood if the prevention of disease is to be really efficient.

It is customary to speak loosely regarding diseases with which parasites are associated, assuming that the parasite is the sole factor with which one need be concerned, whereas other factors may be more necessary to the production of the diseased condition. One evil result of this is that fundamental causes tend to be overlooked and attention concentrated on the obvious factors in the problem, even though these may be of secondary importance. The root rots of forest trees provide good examples of this. In Europe, where conifers are of predominating economic importance, two fungi, *Armillaria mellea* (Vahl.) Fr. and *Fomes annosus* Fr. are pre-eminent as causes of this type of disease. *F. annosus* is acknowledged to be a doubtful parasite (12). The parasitism of *A. mellea* is, however, well established, and all that may be in question is the degree to which it is a parasite. What are the factors in the environment of the tree that predispose it to infection? Are these such as merely enable the fungus to penetrate the host, without in themselves producing in it a morbid condition, or is it necessary for such a condition to exist before the host is unable to resist infection? These are important questions for if it is true that the fungus depends for successful parasitism upon a pre-existing morbid condition in the host, it should be known what such a condition is and how it is brought about. For the means by which this condition is produced is the real cause of disease and should be referred to as such. The importance of speaking thus strictly with regard to disease is that only by so doing is the fundamental cause brought to light and the silviculturist enabled to turn his attention to its removal. If an examination is made of what is known about *A. mellea*, what conclusions must be come to with regard to its status as a parasite?

THE HABITAT OF THE FUNGUS.

A. mellea is strictly a forest fungus and occurs in cultivated land only after it has recently been cleared of woodland or when it borders the forest. Its world-wide distribution, its many hosts, and the loss that it continually causes wherever it is found make it one of the most interesting and widely noticed

of fungi. In one or other connexion it has been described on a number of occasions (11, 12, 14, 5, 3 and 6 *a*). Its general characteristics and those of the disease it causes as a parasite are too well known to need any description, and for the purpose of this discussion I wish to stress only one or two things concerning it. The fungus is subterranean, growing on dead roots and stumps as a saprophyte, sometimes attacking living trees and then growing above the soil, but only beneath the bark of its victims. Once this has dried out it ceases to grow and other fungi may replace it. Its rhizomorphs and the sheets and zones of xylostroma formed in the bark and wood of its hosts are the typical features of its mycelium. Like all fungi a humid atmosphere is a necessity to its existence, but unlike many others it is able to protect itself against dry conditions. Thus the xylostroma after it has become dark coloured has, as one function, the preservation of a highly humid atmosphere within the substratum within which the fungus is growing. The development of this dark-brown colour depends largely on the humidity of the atmosphere. Thus under very humid conditions in tropical rain forest frills of xylostroma that develop in cracks in the bark of cacao are at first cream in colour (5), and similarly rhizomorphs developing in the extremely humid atmosphere of a humidor grow out of agar cream in colour and turn brown only slowly. Under ordinary conditions, of course, only the tip of the rhizomorph is white or cream, the rest being brown. The conditions prevailing within a mass of substratum surrounded by a zone of xylostroma may be judged by the colour of rhizomorphs within and without it. Within the colour is white or cream, without it is brown, as seen growing in agar. In soil that is always moist and where the temperature is always high rhizomorphs may fail to develop (5). The writer also found in growing the fungus on larch leaf debris and sand mixed that in a dry incubator rhizomorphs developed from the small pieces of branch used as inoculating material, but that none developed in a humidor with a very humid atmosphere, filamentous mycelium only appearing.

A. mellea is thus a fungus demanding extremely humid conditions for growth, but which is able to develop under adverse circumstances by means of the protection against desiccation given by its rhizomorphs and xylostroma. For this reason, while it is associated as a parasite with localities that are definitely moist (5, 18, 15), it is at the same time a common parasite in those which have to endure a dry season during some part of the year, whether as a regular occurrence or brought about by occasional severe droughts (1, 3, 6, 16). No survey ever seems to have been made of its ecological distribution. In natural or semi-natural forest it seems to be confined to broadleaved forest, pure or mixed with conifers. In pure natural conifer forest it seems at least to be rare, but in pure conifer plantations established on the site of old broadleaved forest it is extremely common at least during the first rotation.

THE PARASITISM OF *A. MELLEA*.

As a parasite *A. mellea* appears in two roles. First, it occurs as a purely secondary cause of disease—as, for example, on the oak in Europe (6 *b*), *Picea*

morinda in the Himalaya (13), *P. nigra* and *P. rubra* in N. America (4), *P. excelsa* in Central Europe (16), and *Abies pectinata* in Germany (17). Here the primary cause of disease has been drought, defoliation or mildew (oak), drought and sun-search (*P. morinda*), drought (*P. excelsa*), defoliation and drought (*P. nigra* and *P. rubra*), and an undetermined cause in the case of *A. pectinata*. In its second role, it appears to act as a virulent parasite killing healthy trees, and it is noteworthy that when so acting the fungus is always reported as attacking crops that have been artificially regenerated or grossly interfered with by mankind (3, 5, 6 *a*, 8, 10, 15, 16). It is quite possible that in natural forest the fungus frequently acts in this second role, but if this has been observed it does not appear ever to have been recorded. Is the fungus really a virulent parasite on healthy trees, and why does it so frequently appear to assume this role in artificially established forest and in plantations? There are two lines of inquiry that will help to throw light on these questions. The first seeks to determine what factors are associated with attack by *A. mellea* on apparently healthy trees; the second to establish what is the relative susceptibility of different hosts, and whether the degree of susceptibility ever varies.

THE FUNGUS AS A FACTOR IN THE DISEASE.

It is obvious that unless the fungus is present it cannot attack the tree, but what is much less obvious is whether, if the fungus is present and actively developing, a host, ordinarily stated to be susceptible, will of necessity become infected. It may be noted here that wounds or dead roots are not necessary to enable the fungus to enter a host (6 *a*, 22). Accordingly even if no wounds or dead roots are present a susceptible host is still liable to be infected. Any observations, therefore, will be of value which go to show that in the presence of the actively developing parasite a species may be at one time susceptible and at another resistant.

There is practically no evidence of the fungus growing in direct contact with the living uninjured tissues of possible hosts and yet failing to bring about infection. The writer has, however, observed young developing rhizomorphs growing in the bark at the base of Corsican pine and *Thuja plicata* without the trees in any way being affected. Rhizomorphs have also been observed tightly encircling young Douglas fir without penetrating the trees. All these species are known to be attacked, and, as a matter of fact, were situated in the same wood and on similar soil to specimens of all three species that had definitely been infected. There is much more evidence of conifers having been infected and yet surviving without their growth being in any obvious way checked. Berger (2) observed this on N. spruce in Germany, also Craighead (4) on spruce in Canada, and numerous instances are known to the writer (6 *a*). Cases of this are probably common on broad-leaved species, as on aspen in Sweden (7) and U.S.A. (19), where the fungus causes a butt rot. Geschwind (10) reports this phenomenon also, and the writer has observed it on willow (*Salix alba*), a tree which sometimes succumbs to attack. Altogether there is therefore fairly good evidence that the mere presence of the fungus does not mean that trees will

of necessity be infected and that even when once successfully infected the host may become resistant again. Apart from this there is a great deal of indirect evidence to show that the fungus may be actively growing in the presence of species considered susceptible and yet fail to attack successfully, or only succeed in doing so during a limited period in the life of the crop. Much of this will come forward when discussing susceptibility of species of host.

Taken as a whole the evidence here put forward points to the conclusion that the main factor in deciding whether a host is or is not susceptible is at least not the fungus. For were the fungus capable of killing healthy trees it could hardly fail to cause the death of any that belonged to a species known to be commonly susceptible once it had already infected them. In order to understand the disease it thus becomes necessary to seek the chief causes of susceptibility in factors external both to the host and its parasite. Such factors are chiefly to be sought either in the condition of the soil or in the silvicultural state of the forest. Both of these will now be discussed in relation to susceptibility to infection.

THE CONDITION OF THE SOIL.

As *A. mellea* is a fungus attacking the roots of trees and living in the soil, it is to be expected as probable that any adverse soil condition will heighten the susceptibility of its hosts to infection. When trees that have suffered from drought are infected this is obviously what has happened. Are adverse soil conditions commonly associated with susceptibility to the fungus when attacking apparently healthy trees? Certain cases have been described giving evidence with regard to this. Thus Dade (5) found that the collar crack disease of cacao only became epidemic on level sites with a very high atmospheric humidity and a high soil moisture. On sloping well drained sites death was only sporadic and the losses relatively insignificant. Also Butler (3) found that in tea plantations where the soil was not protected from being washed away by heavy rains and its fertility had become low, *A. mellea* caused serious loss; but where proper care was taken to maintain the fertility of the soil death was only sporadic. Here are two clear cases in which under adverse soil conditions the fungus is a virulent parasite but where under less adverse conditions it becomes very much less virulent. With regard to forest trees no such direct evidence is available. Sometimes, however, these become susceptible under conditions that of necessity involve adverse soil conditions as at least a partial cause. Thus Geschwind (10) observed that in a mixed forest of beech, pine, spruce, and silver fir, *A. mellea* acted as a parasite only after beech had been extracted in preference to other species, with the result that the forest became to consist purely of conifers. The gaps left by the beech failed to fill up with regeneration, became weed covered and gradually the death of the surrounding conifers, owing to infection by *A. mellea* began to take place. The shallow-rooted spruce was affected first, the pine and silver fir being taken later. The change in condition of the forest described here is one that is notoriously accompanied by deterioration in soil fertility and which all foresters in Europe

strenuously try to prevent taking place. This case, therefore, falls into line with the tea and cacao as an attack following or accompanied by deterioration in soil condition.

As in plantations, the moisture content of the forest soil affects susceptibility to infection. Thus Frömbling (8), without giving any details, states that infection by the fungus is associated with very moist soil conditions, agreeing in this with Dade (5), Miège (15), and others. It has been noted already that infection is frequently associated with unduly dry soil conditions, but here it almost certainly occurs after and not during the dry period. Sometimes it may be a definite advantage to have a soil which is always moist, either on account of its power of retention of water or because of the height of the water table. Thus Craighead (4) notes that a correlation seems to exist between abundance of available water and the recovery of spruce and balsam fir from defoliation by the spruce bud-worm. Trees standing in localities in which the soil tended always to be moist recovered to a much greater extent than those on the drier sites. As almost every tree appears to be given its *coup de grâce* by *A. mellea*, it follows that resistance to fungal infection must have depended on the degree of soil moisture. Or perhaps it would be truer to say that upon this depended the ability of the tree to remain sufficiently alive during a period of stress to be resistant to the fungus afterwards.

It is thus seen that where the matter has been investigated or any data given from which the soil conditions may to some extent be deduced, susceptibility or resistance to infection depends largely on the extent to which these favour the development of the tree.

THE SILVICULTURAL STATE OF THE FOREST.

The relationship between the silvicultural state of the forest and infection by *A. mellea* has really never been investigated. That such a relationship does exist can be seen from the case quoted above as described by Geschwind (10). There bad silviculture, or perhaps more truly lack of silviculture, ultimately reduced the forest to such a state that infection became possible. It is probable that the importance of any silvicultural practice lies chiefly in its effect on the soil, and the same practice may not have an equally good effect on all types of soil. It is in this way that apparently contradictory opinions arise. Thus Oppermann (18) writing of spruce (*P. excelsa*), and Wiedemann (21) of conifers in general, recommend that dense stands should be avoided in order to keep down the losses caused by fungi such as *A. mellea* and *F. annosus*; while Frömbling (8) seems to consider the fungus much more innocuous in dense spruce stands than in more open ones. It is apparently also the experience of the latter author that the use of transplants in the artificial regeneration of spruce is accompanied by serious loss owing to *A. mellea*, and he recommends regeneration by sowing *in situ*, for he considers that by this means loss will be avoided. It is, however, by no means a general experience that Norway spruce or any other conifer that is regenerated by the use of transplants always suffers serious loss in this way, and it can only be that special soil conditions account

for the variety of experience. Another phenomenon which points to the association between silvicultural and soil conditions in relation to infection by the fungus is the occurrence at particular stages in the growth of the crop of susceptibility to infection. Thus Hiley (12) notes that larch in England very frequently suffers serious loss at about the age of 15 years. Nechleba (16) finds spruce most susceptible at about 25 years, while Frömbling (8) on the contrary finds it to be most susceptible in the first years after planting and to become less susceptible as the canopy closes. When it is remembered that the fungus is present during the whole time, whether trees are infected with it or not, and that apart from exceptional occurrences, such as drought or defoliation, the chief factor causing alterations in the environment is the crop itself, it can be seen that the manner of regeneration, the degree of thinning and the choice of species may not be without a considerable influence in bringing about susceptibility to infection.

VARIATION IN SUSCEPTIBILITY TO *A. MELLEA*.

It has long been known that different species of host vary in susceptibility to *A. mellea*. Thus broad-leaved trees are generally accepted as being more resistant than conifers. Among the latter many apparent degrees of susceptibility occur, and there are probably many different opinions among foresters as to what those are. Thus in Germany, Hess, as quoted by Nechleba (16), considered Scots pine to be more susceptible than Norway spruce. Nechleba's own experience and also that of Frömbling (8) was exactly the opposite. In Britain it is usual to find Scots pine the more susceptible; indeed, there pines in general seem to be the most susceptible of all species of conifer. Now variations in susceptibility may be, and doubtless often are, caused by variations in the environment in different localities. Thus epidemics of collar crack in cacao may occur in one place but not in another, and the varying conditions of the respective localities account for this. Similarly, among conifers it has been found that in the presence of an abundant development of the fungus a species may be attacked in one place but not in another. Thus within the writer's experience Japanese larch is resistant near Oxford during the first few years after planting, but has proved to be very susceptible in Shropshire. The unknown cause of this is almost certainly some difference between the two localities in environmental conditions. Of equal interest are the variations in susceptibility occurring in a species in any one place and during one rotation. Thus Hiley (12) refers to the increase in susceptibility of larch at about the age of 15 years. Changes in susceptibility have also occurred in the experimental plots in Bagley Wood, Oxford, referred to by him. The Sitka spruce have ceased to die even though in one or two cases trees are known to have roots infected with the fungus. In the Corsican pine, where only one tree had been killed, a considerable number have been lost, but since the plot has been thinned, both officially and accidentally by fungus, the rate of death has slowed up and the attack is apparently stopped. In the Norway spruce two have died, but others have been attacked, yet still live and grow apparently

without check. The high death-rate in the Weymouth pine has not been kept up. One of the Douglas fir and many of the *Thuja plicata* and *Tsuga heterophylla* have been infected but not killed. In the case of *Thuja*, *Tsuga*, and larch, infection has occurred subsequently to dry periods in 1919 and 1921 and appears to be secondary to damage by drought.

These few examples will be sufficient to show that even where the fungus is abundant, as everywhere in Bagley Wood, the susceptibility of any one species is not constant in degree over any length of time but varies with comparative frequency. This undoubtedly points to something external to both the host and the parasite which controls susceptibility otherwise, as in the case of Sitka and Norway spruce, infected trees would not die on one occasion and not on another. It is also confirmation of Hiley's statement that 'if perfectly healthy roots were liable to be penetrated by the rhizomorphs, I do not think that such immunity (to infection on the part of various species) could have been expected' (12).

Very important for this discussion is the conception of what a perfectly healthy root is. Usually it is considered that any root is healthy that belongs to a tree that as a whole appears itself so to be. This is, however, not of necessity true, and an example may be quoted in illustration. Two Corsican pine occurred in Bagley Wood, both with rhizomorphs growing in the thick bark at the root collar. The one was a dominant tree and very vigorous. It had not been infected and there were no signs of attempted attack. The other tree grew on similar soil and only a short distance away. It appeared to be healthy, but was just becoming dominated by the surrounding trees. This tree was discovered to be quite recently penetrated by the fungus through uninjured cork layers. The probable explanation is, of course, that the tree had become debilitated owing to its inferior position and so was unable to resist infection. This explanation, however, introduces a more refined conception of a state of disease, for if the tree had become debilitated, this state of debilitation was not merely a condition predisposing the tree to infection but was in itself a state of disease. Once this conception is realized it can be seen that susceptibility to infection may be the result not merely of catastrophies such as drought or being planted in an excessively wet soil, but that less obvious things may bring it about. In this way the number of possible adverse factors that might arise in the environment of the plant are, quite apart from possible variations in the inherent resistance of the host or in the virulence of the fungus, sufficiently great to account for all variations in susceptibility that might occur.

CONCLUSION.

It is now possible to attempt to answer the questions asked during the course of the discussion. First, is the fungus really a parasite infecting healthy trees? While there is no proof that it never does act in this way, all the evidence goes to show that it is always secondary to some other factor acting as the primary cause of disease. If the fungus is a parasite of a secondary nature, what are the

factors predisposing the trees to its infection and bringing about the initial state of disease? It has been shown that in many cases these are adverse soil conditions acting alone or in conjunction with others such as defoliating larvae or infection by mildew. Sometimes the latter may of themselves cause susceptibility. These initial causes of disease are not always obvious, but it is to be presumed, in lack of evidence to the contrary, that they are always there when trees become infected. It remains to ask why it is that the fungus appears to so great an extent as the apparent primary cause of disease in artificially regenerated forest or plantations. Once it is granted that the fungus is always acting in a secondary role, this question needs to be asked no longer. The difference between natural and semi-natural forest and that artificially regenerated is that in the one case the primary cause of disease appears usually to be some obvious thing such as drought or defoliation, while in the other it is more difficult to observe and so more frequently remains undetected. What is needed, then, in order to come to a greater understanding of the origin of susceptibility to root-rotting fungi such as *A. mellea* is a greater knowledge of the reaction of the forest tree to its environment. In times when new species are constantly being introduced in many parts of the world and grown for economic purposes outside the range of their natural distribution this is particularly necessary, for much of the disease that affects such species is caused by nothing more than a failure to realize what are the conditions necessary for their healthy growth.

The importance of understanding what is necessary for the health of the crop is so obvious that it should need no stressing. The subject is, however, so large that it is only by degrees that a proper comprehension of it will be obtained. Nevertheless, it will in the meantime be an advantage if it comes to be increasingly understood that the study of forest disease is not a pure mycological or entomological matter, but that it is, as a whole, based on an understanding of the life of the forest and especially on the normal and pathological physiology of the individual trees. Health or disease involve a particular way of life, that is for the tree particular conditions for growth, and while it may in some cases pay to grow crops that are unsuited to the conditions within which they grow and to protect them artificially against disease, in forestry this will not usually be so. Everything depends, therefore, in having a crop that is really suited to its environment, and it is in endeavouring to determine what this is that the pathologist and silviculturist meet and real progress is made in the control of forest disease.

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